THE DEMISE OF THE DANCING DINOSAURS?

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ABSTRACT

Speed-estimates derived from fossil trackways have recently been used to support the claim that dinosaurs were warm-blooded. Critical examination of those speed-estimates reveals no basis for the claim that "dinosaurs cruised at warm-blooded speeds": the speeds of dinosaurian track-makers appear to have been consistently overestimated, and comparisons of absolute speed are inappropriate because they make no allowance for differences in size of the track-makers. If size-differences are taken into account, dinosaurs do not appear to be significantly faster, or slower, than other terrestrial vertebrates.

KEYWORDS: dinosaurs, tracks, speed, locomotion, thermal physiology.

INTRODUCTION

The protracted and lively debate about "warm-blooded" *versus* "cold-blooded" dinosaurs was initiated nearly 20 years ago in a provocative paper by Bakker (1972). Despite a great deal of discussion, the issue remains unresolved and continues to generate controversy (e.g. Thomas & Olson 1980; Bakker 1986a; Ostrom 1987; Reid 1987, 1990).

Bakker's original argument for dinosaurian endothermy (1972) drew on three categories of evidence - (1) bone histology, (2) features of gross anatomy (e.g. locomotor adaptations, pneumatopores, secondary palate), and (3) community structure. Evidence from those same three sources has been amplified considerably and combined in various permutations in Bakker's subsequent publications on dinosaur biology (e.g. Bakker 1974, 1975a, 1975b, 1980, 1986a).

More recently, the claim that dinosaurs were warm-blooded has been bolstered with the evidence of speed-estimates derived from fossil trackways (Bakker 1986a, 1986b, 1987; Paul 1988). The fullest treatment of this evidence is given in Bakker's article titled "The Return of the Dancing Dinosaurs" (1987). Briefly, Bakker ascertained that the average walking speeds ("cruising speeds") of dinosaurs and thecodontians were at least as great as those of

existing mammals. By contrast, average walking speeds were found to be "much lower" among undoubted ectotherms (living amphibians and reptiles, along with a variety of Permian and Carboniferous tetrapods). In Bakker's estimation these findings (Fig. 1) demonstrate that "dinosaurs cruised at warm-blooded speeds" (1987: 39).

Although the evidence of dinosaur tracks is only a small ingredient in the overall argument favouring dinosaurian endothermy, it does nevertheless comprise hard quantitative data and should, for that reason, provide some fairly robust conclusions. Moreover, a recent resurgence of interest in the study of dinosaur tracks and their biological significance (Haubold 1984; Gillette and Lockley 1989; Thulborn 1990; Alexander 1991) provides a satisfactory background for appraising the validity and the significance of Bakker's findings.

VALIDITY OF SPEED-ESTIMATES

Bakker estimated the speeds of dinosaurs and other extinct tetrapods by means of a method pioneered by Alexander (1976). That method certainly seems to provide realistic estimates of speed, though Alexander conceded (1989: Fig. 6) that it might tend to underestimate moderate speeds and to overestimate higher ones. In this
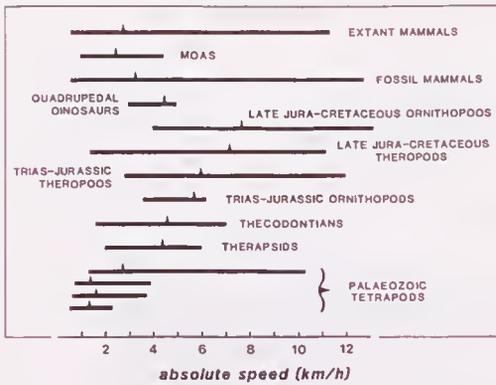
Fig. 1. Estimated 'cruising speeds' of extinct tetrapods and observed 'cruising speeds' of living mammals. Range and median indicated for each group. Diagram adapted from Bakker (1987: Fig. 7), with sample for 'Late Jura-Cretaceous theropods' excluding an outlier of speed estimates for running animals (Farlow 1981).

context it may be noted that the highest estimates of speed obtained by Bakker are those for dinosaurs (Fig. 1).

In order to check the accuracy of Alexander's (1976) method, Bakker plotted predicted speeds against observed speeds for a range of extant tetrapods (1987: Fig. 4). This test revealed that "ninety-five percent of the predictions fell within 2 times the actual speed" (Bakker 1987: 48). While this test confirmed the value of Alexander's method *as a generalization*, it did not sanction the uncritical application of that method to "cruising speeds" in particular. Here it must be observed that Bakker's test confirmed the reliability of Alexander's method over a very wide range of speeds, from about 0.7 km/h (walking lizard, *Teratoscincus*) to more than 90 km/h (fast-running cheetah). But within the restricted range of "cruising speeds" discussed by Bakker (approximately 0.5 to 12.1 km/h), Alexander's method would seem to be a far less reliable predictor of actual speed. And within the extremely narrow range of median "cruising speeds" calculated by Bakker (approximately 1.3 to 7.7 km/h), Alexander's method appears to be a very poor predictor indeed.

Thus, Bakker's (1987) predictions of speed for dinosaurs and other extinct tetrapods are not necessarily accurate, despite the fact that Alexander's (1976) method was confirmed as a reliable generalization. Unfortunately, Bakker's presentation of his findings (Fig. 1) gave no indication of the possible margins of error. The reliability of those findings would have been more readily apparent had they been presented as mean values with confidence limits, rather than simple histograms with median values.

Prerequisites for the use of Alexander's method are measurements of stride length, SL, and of the track-maker's height at the hip, h. Stride length is measured directly on the trackway, but height at the hip must be estimated, usually from the size of the track-maker's footprints. Obviously the dimension h must be estimated with care, since any error may have a substantial effect on the ratio SL/h and, hence, on the final prediction of the track-maker's speed.

Numerous methods, some more reliable than others, have been used to estimate h for dinosaurian track-makers (Thulborn 1990: 249-256). Bakker estimated h by means of simple morphometric ratios, where "hind-limb length" (equivalent to h) was expressed as a multiple of "foot breadth across the metatarsals" (1987: 48). So, for instance, sauropods (brontosaurs) were estimated to have hindlimbs equivalent in length to about 4.8 times the width of the metatarsus. Unfortunately, Bakker's list of such ratios was neither complete nor very detailed: it gave no ratio(s) for theropod dinosaurs, and it specified a wide range of ratios for ornithopod dinosaurs - from 5.8 in hadrosaurs to 8.0 in fabrosaurs. Nor did Bakker explain how estimates of "foot breadth across the metatarsals" were derived from fossil footprints. Such explanation is essential because there seems to be no immediately obvious corre-
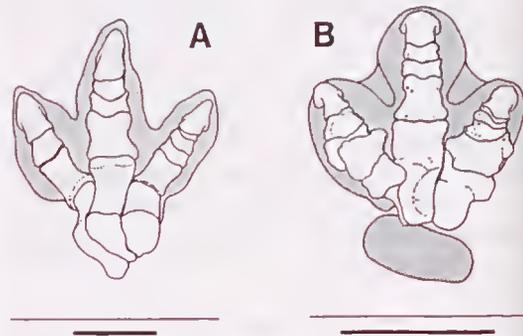

Fig. 2. Foot skeletons of large ornithopod dinosaurs superimposed on corresponding footprints. A, Foot skeleton of the early Cretaceous ornithopod Iguanodon superimposed on footprint from rocks of similar age (adapted from Dollo 1906). B, Foot skeleton of the hadrosaur Hypacrosaurus superimposed on a suspected hadrosaur footprint from the Upper Cretaceous of Alberta, Canada (adapted from Langston 1960). Note that there is no straightforward correspondence between the maximum width of the metatarsus (thick bar) and the maximum width of the footprint (thin bar).

lation between the width of a dinosaur's footprint and the width of its metatarsus (Fig. 2).

Bakker's reliance on morphometric ratios disregards the prevalence of allometry within dinosaur taxa: it assumes that all individuals within a dinosaur taxon will share an identical ratio of foot breadth/hindlimb length, regardless of their size or ontogenetic status. That assumption is unrealistic and is likely to generate some spurious estimates of h and, therefore, of the trackmakers' speeds (Thulborn 1989, 1990). While estimates of h derived from morphometric ratios are undeniably convenient for preliminary analyses of tracky data, they are probably less reliable at the level of accuracy required by Bakker's investigation.

Moreover, it is difficult to confirm the absolute values of the morphometric ratios cited by Bakker (1987). For example, the only well-known skeleton of a fabrosaurid dinosaur, *Fabrosaurus australis* (*Lesothosaurus diagnosticus*) has a skeletal hip height of 30.2 cm, representing the combined lengths of femur, tibia and metatarsus (Thulborn 1972); the maximum width of the metatarsus is 2.3 cm, indicating that the ratio of hindlimb height to metatarsus width is roughly 13/1 and not, as Bakker suggested, 8/1. Measurements from two specimens of the primitive-looking ornithopod dinosaur *Hypsilophodon foxii* (Galton 1974) provide ratios of 9/1 and approximately 10/1. In the case of these smaller ornithopods, including fabrosaurids, it appears that Bakker has underestimated the length of the hindlimb, thus generating overestimates of speed. (I assume that estimates of hindlimb height exclude the digits; if the digits are included, the discrepancies are even more pronounced, with *Fabrosaurus* having a ratio of nearly 16/1.)

Similar queries arise over Bakker's estimates of hindlimb length for sauropods (brontosaurs) and hadrosaurs (duck-billed dinosaurs). Among the hadrosaurs, for instance, one survey of osteometric data indicates that h is approximately 5.9 times the length of the metatarsus (Thulborn 1989: 42). Since the hadrosaurian metatarsus is between 1.1 and 1.3 times wider than long, h might be estimated at roughly 6.4 to 7.5 times metatarsus width. By contrast, Bakker (1987: 48) cited a figure of 5.8 times metatarsus width. Here, again, it seems that the morphometric ratio used by Bakker would consistently generate underestimates of size and overestimates of speed.

SIGNIFICANCE OF SPEED-ESTIMATES

Bakker claimed that cruising speeds were much lower among ectotherms than among living mammals (1987: 49), yet this is clearly not the case. Figure 1 shows that the median cruising speed of existing mammals (nearly 3 km/h) is not significantly higher than among Palaeozoic tetrapods (with median predictions ranging from about 1.5 km/h to 3 km/h). Here it should be recalled that the the predictions in Fig. 1 were guaranteed to be no more accurate than "within 2 times the actual speed" (Bakker 1987: 48).
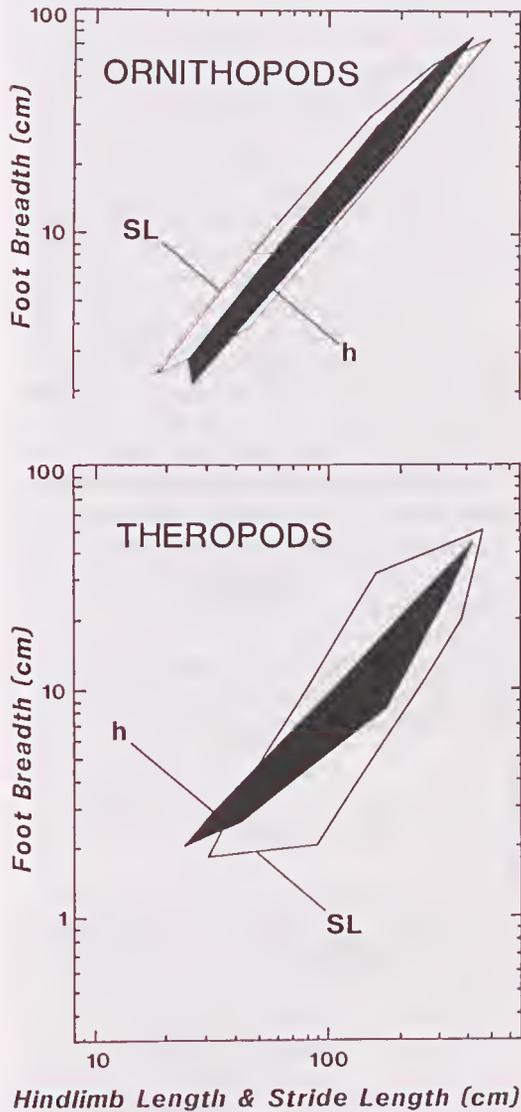

Fig. 3. Relationship of stride length (*SL*) to hindlimb length (*h*) in ornithopod dinosaurs and theropod dinosaurs. Both diagrams adapted from Bakker (1987: Fig. 6).

Thus, Bakker's basic assumption - that endothermic tetrapods *should* cruise at higher speeds than ectothermic tetrapods - seems less than convincingly demonstrated.

It is well known that a small animal needs to achieve a higher level of locomotor performance (i.e. a faster gait) in order to match the speed of a bigger animal (Heglund et al. 1974; Thulborn and Wade 1984). This point is easily appreciated by small children, who are often obliged to trot alongside their walking parents. Nevertheless, Bakker (1986a, 1987) compared estimates of absolute speed for dinosaurs and other tetrapods regardless of their body size (Fig. 1). Bakker clearly appreciated the significance of size, since he claimed (1987: 48) that "dinosaurs had cruising speeds as high or higher than that [sic] of mammals with comparable body size". Yet, even so, his findings were presented (1986a,b, 1987) only in terms of absolute speed. Those findings might be expressed more appropriately, and more meaningfully, in terms of dimensionless speed $(u[gh]^{-0.5})$, Froude number (u^2/gh) or relative stride length (SL/h) - where u is velocity (m/s) and g is the gravitational constant (Alexander 1976, 1977, 1991; Thulborn and Wade 1984). Any of these various measures will permit more equitable comparisons of locomotor performance among animals of different size. Here it is most convenient to make comparisons in terms of relative stride length (SL/h), because estimates of this ratio are commonly cited in studies of dinosaur tracks.
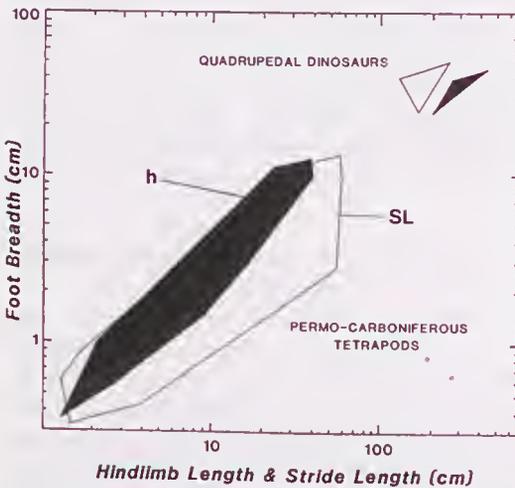
In terms of relative stride length, Bakker's findings (1987) appear to be entirely consistent with other studies on dinosaur locomotion (e.g. Thulborn 1982, 1984). For instance, Bakker showed (1987: Fig. 6) that stride length (SL) is roughly equivalent to hindlimb length (h) throughout the bipedal dinosaurs, both ornithopods and theropods (Fig. 3); this finding is in fair agreement with the observation that average stride length was equivalent to about 1.3h among bipedal dinosaurs in general (Thulborn 1984).

In addition, a definite pattern begins to emerge if one compares estimates of size and stride length for the smallest animals and the largest. For the smallest animals considered by Bakker (Permo-Carboniferous tetrapods), stride length is consistently as great or greater than height at the hip; by contrast, the biggest animals (quadrupedal dinosaurs and elephants) took strides noticeably shorter than their height at the hip (Fig. 4). The changeover from long strides in small animals to progressively shorter strides in bigger animals is also apparent within Bakker's sample of data for theropod dinosaurs alone (Fig. 3). These findings confirm the existence of a negative correlation between relative stride length and body size (Thulborn and Wade 1984: 448), and they underline the need for Bakker's estimates of absolute speed to be scaled or adjusted in accordance with body size.

The real significance of Bakker's findings (1986a, 1987) is most easily appreciated from
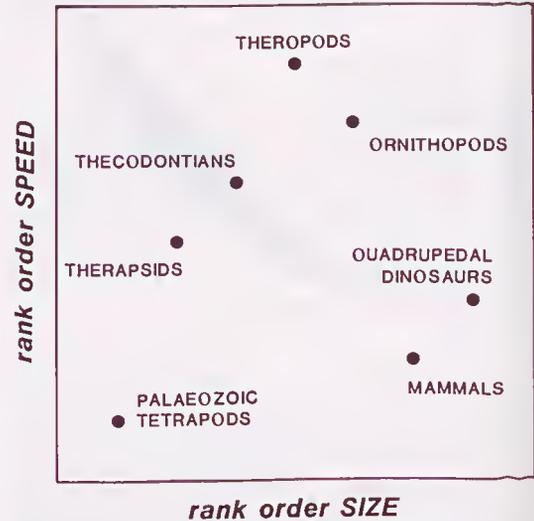

Fig. 4. Relationship of stride length (SL) to hindlimb length (h) in Palaeozoic tetrapods and quadrupedal dinosaurs. Note progressive decrease in relative stride length (ratio SL/h) in bigger animals. Adapted from Bakker (1987: Fig. 6).

Fig. 5. General relationship of absolute speed (median estimate) to body size (median estimate of h) in dinosaurs and other tetrapods. Derived from data presented by Bakker (1987: Figs 6 and 7).

Fig. 5, where median estimated speed is plotted against median body size. Evidently the smallest and largest animals have the lowest absolute speeds whereas animals of intermediate size (which happen to be dinosaurs) attain the highest absolute speeds. This pattern of relationship between size and speed probably reflects the well-known fact that there is an optimal body size for terrestrial locomotion. In terms of running ability for tetrapods in general, Coombs (1978) considered the optimum to be about 50 kg; for mammals alone, Garland (1983) specified an optimum of 119 kg. The optimal body size probably furnishes an advantageous ratio of muscular power to body mass (proportional to the ratio of cross-sectional area to volume); the power/weight ratio is advantageous in the sense that it can be exploited by means of cursorial adaptations (Coombs 1978). Smaller animals have an even more favourable ratio of power to weight, but they do not attain very high speeds on account of their small absolute size - which probably restricts maximal stride length. At the other extreme, big animals tend to be relatively underpowered, since the power/weight ratio declines rapidly as body mass increases.

In short, Bakker's study of fossil trackways (1986a, 1987) does not support the claim that dinosaurs were warm-blooded. Bakker's estimates of absolute speed may not be sufficiently reliable to demonstrate meaningful similarities or differences; moreover, there is some likelihood that the speeds of dinosaurian track-makers have been consistently overestimated. Even if all Bakker's findings (Fig. 1) were acknowledged to be unquestionably correct, they still would not demonstrate that dinosaurs were warm-blooded: those findings merely demonstrate the well-known fact that there is an optimal body size for terrestrial locomotion (Fig. 5).

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